

STRUCTURE AND ONTOGENY OF STOMATA IN POLYPODIACEAE

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Rijksherbarium, Leiden.

SUMMARY

The stomata as occurring on the fronds of the sporophytes of a large number of *Polypodiaceae* s.s. (Filicales) are investigated. A number of different stomatal types is recognised, (newly) described, and their ontogeny investigated. The different types of stomata are discussed in relation to their possible significance for tracing phylogenetic relationships in the *Polypodiaceae* following a cladistic analysis.

INTRODUCTION

The ferns presently included in the *Polypodiaceae* (i.e. *Polypodiaceae sensu* Copeland, 1947, but excluding the taxa transferred elsewhere by Crabbe et al., 1975) are basically epiphytic and almost wholly tropical in distribution. They are characterised by the possession of exindusiate sori, sporangia with a stalk composed of more than one but always less than four rows of cells, and bilateral spores with a more or less distinct perispore. The family with its vast wealth of species and generous diversities has undergone many taxonomic vicissitudes and splitting especially since the time of Diels (1902) and Christensen (1905). Many heterogeneous elements like the dipteroids, cheiroleuroids, loxogrammoids and grammitoids have meanwhile been removed from it, yet the family has not attained reasonable taxonomic stability. Pteridologists not only differ on the propriety of retention of some of the remaining members in the family, but also on the recognition and delimitation of many of its genera some of which appear ill-defined. Disagreements prevail even about the position of the family in relation to other ferns (Holtum, 1973; De la Sota, 1973, and Pichi Sermolli, 1977). These taxonomic disagreements are certainly due to our ignorance about the true phylogenetic relationships of this family.

It was, therefore, felt that most of the essential data on the structure and ontogeny of different plant parts of the representatives of the genera and their allies must be available and brought together before opening the way of serious taxonomic revision of the family. This paper on stomata is the first of a series of reports on the structure and ontogeny of different properties of the polypodioids which are now being investigated at the Universities of Leiden, Utrecht, and Kalyani. It includes

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apart from confirmation of some previous reports (Van Cotthem, 1970a; Fryns-Claessens and Van Cotthem, 1973), new findings regarding the stomatal structure and ontogeny and structure of the stomata of many species. Further, parts of our observations differ in many important respects from those of previous authors (Van Cotthem, 1970a and 1973; Fryns-Claessens and Van Cotthem, 1973; Pant, 1965; and Mickel and Lersten, 1967). As a result, it appeared possible to describe two new stomatal types, and to reconstruct the probable pathways of evolution of the stomatal types recognized in the family, for the first time.

ACKNOWLEDGEMENTS

It is with pleasure that U.S. records his gratitude to Professor Dr. C. Kalkman who made it possible for him to come to Leiden to work on this project and for placing at his disposal the facilities of the Rijksherbarium. He would particularly like to thank the Netherlands Organization for the Advancement of Pure Research (Z.W.O.) for financing his one year stay in the Netherlands. His thanks are also due to Dr. W. Jülich for his various help, co-operation, and interest in the work.

We would like to express our sincere thanks to Mr. G. J. de Joncheere for his valuable comments, help with nomenclature, and determination of taxa investigated in these studies. We are indebted to the authorities of the Leiden Botanical Garden and also to Mr. A. Mulder for providing material for ontogenetic studies from plants under cultivation in the phytotron.

MATERIAL AND METHODS

Except a few cases where preserved material was available, herbarium specimens located mainly at the Rijksherbarium, Leiden, were used to survey the stomatal types. Frond segments were boiled in water, fixed in F.A.P.A. (40% formalin: 5, glacial acetic acid: 2.5, propionic acid: 2.5 and 50% alcohol: 90), and macerated overnight at 58 °C following Franklin's method in equal volumes of 20% hydrogen peroxide and concentrated glacial acetic acid. These were stained in Sudan IV in 70% alcohol and finally mounted in glycerine-jelly. Slides for references are kept in the Rijksherbarium, Leiden. Replicas of epidermal surfaces were also made with cellulose acetic sheets and acetone (Payne, 1968).

For ontogenetic studies fronds at various stages of development were collected from plants grown in a climate chamber (phytotron) located in the Leiden Botanical Garden, fixed in F.A.P.A., and stored in 70% alcohol. Temporary acetocarmine mounts of epidermal peels were made. Epidermal peels stained with Delafield's hematoxylin or Sudan IV in 70% alcohol were also examined. Illustrations were made with the aid of a Leitz drawing apparatus.

The terminology used by Van Cotthem (1970a, 1970b) is adopted here with some modifications. For indicating the types of stomata in various taxa, Copeland's (1947) system of classification — but excluding the taxa transferred elsewhere by Crabbe et al. (1975) — is followed only for practical purpose. The reason for choosing Copeland's system is due to the fact that this system of classification is still being widely used by pteridologists all over the world despite many demerits. We have, however, recognised *Phymatodes* as a genus distinct from *Microsorium* though Copeland (1947) indicated that as a matter purely of convenience. *Drymoglossum* is used instead of *Pteropsis*.

OBSERVATIONS

In most of the species investigated the guard cells are in the same level with the epidermis, but in many species of *Pyrrosia* they are deeply sunken in the mesophyll

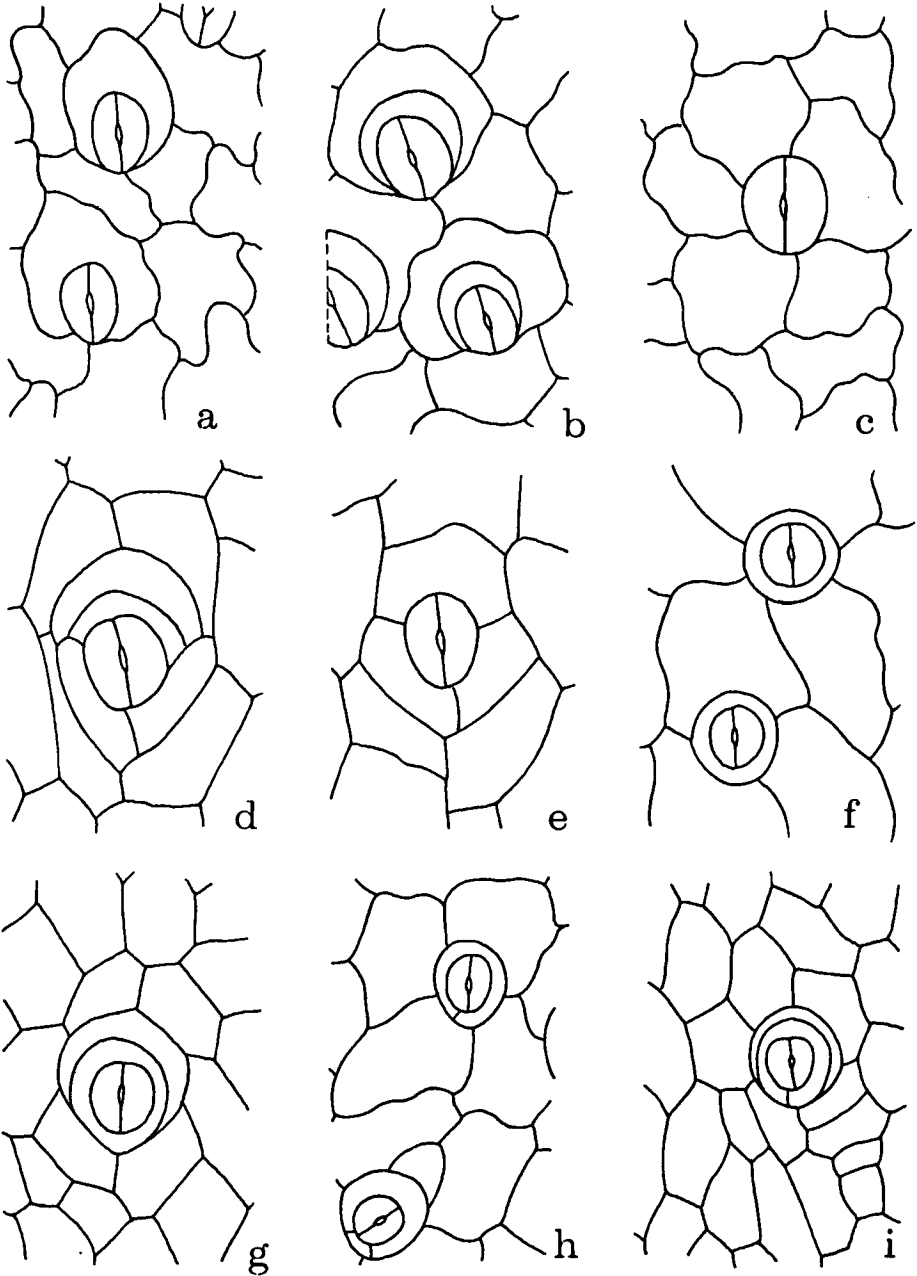


Fig. 1. Epidermis in surface view illustrating polocytic (a), copolocytic (b), anomocytic (c), cocyclocytic (d), cyclocytic (e), pericytic (f), copericytic (g), desmocytic (h) and codesmocytic (i) types of stomata. — a. *Selliguea feei*. — b. *Colysis membranacea*. — c. *Polypodium fallax*. — d. *Lemmaphyllum microphyllum*. — e. *Lemmaphyllum rostratum*. — f. *Pyrrosia flocculosa*. — g. *Drymoglossum piloselloides*. — h. *Platynerium quadridichotomum*. — i. *Platynerium alaicorne*. — (A11 \times 750).

forming an external respiratory cavity. In no species investigated the guard cells with their neighbouring cells are found to protrude outwards above the general level of the epidermis. The fronds in most of the species are hypostomatic. The amphistomatic condition has only been found in *Platyserium grande*, *P. holttumii*, *P. stemaria* and *P. superbum*. The stomata are generally evenly distributed and oriented in the direction of the long axis of the frond. Only occasionally, in some discrete areas, they become irregularly oriented. Two or more stomata rarely become laterally contiguous but polar contiguity in them has never been observed. Nine basic stomatal types are here recognised in the family. These are classified on the basis of the number of subsidiary cells and the mode of orientation of the surrounding cells, as follows:

1. *Polocytic type* — stoma (i.e. the two guard cells and the encircled stomatal pore) surrounded by a single, easily recognisable, U-shaped subsidiary cell; anticlinal cell walls of the guard cells and the subsidiary cell linked together towards the distal end (Fig. 1, a).

2. *Copolocytic type* — stoma of the polocytic type with an additional subsidiary cell partly enclosing the first; the anticlinal cell wall of the two subsidiary cells linked together towards the distal region (Fig. 1, b).

3. *Anomocytic type* — stoma surrounded by a few cells not differing from other epidermal cells in form and size (Fig. 1, c).

4. *Desmocytic type* — stoma completely encircled by a subsidiary cell; the subsidiary cell and any one of the guard cells or both of them connected at the distal region by one or two anticlinal cell walls (Fig. 1, h).

5. *Codesmocytic type* — stoma of the desmocytic type with an additional subsidiary cell; anticlinal cell walls of the two subsidiary cells linked together at the distal region (Fig. 1, i).

6. *Pericytic type* — stoma surrounded by a subsidiary cell; guard cells and the subsidiary cells not linked together by any anticlinal cell walls (Fig. 1, f).

7. *Copericytic type* — stoma of the pericytic type with a second subsidiary cell; the periclinal walls of the two subsidiary cells linked at the distal region (Fig. 1, g).

8. *Cyclocytic type* — stoma surrounded by 3 or more elongated neighbouring cells apparently forming a cycle of cells (Fig. 1, e).

9. *Cocyclocytic type* — cyclocytic stoma with an additional layer of encircling cells at least at the proximal end if not throughout (Fig. 1, d).

DISTRIBUTION OF DIFFERENT TYPES OF MATURE STOMATA

The types of mature stomata found in different taxa studied are indicated in the table below (+ = stomatal types present; + + = stomatal type more abundant than the other associated type or types; (+) = stomatal type infrequent):

	polo	copolo	anomo	desmo	codesmo	peri	coperi	cyclo	cocyclo
<i>Aglaomopha</i>									
<i>meyeniana</i>	+	++							
<i>splendens</i>	+	+							
<i>Anapausia</i>									
<i>decurrens</i>	+	+							
<i>Arthromeris</i>									
<i>himalayense</i>	+	+							
<i>lehmanni</i>	+	+							
<i>wallichiana</i>	+	+							
<i>Belvisia</i>									
<i>annamensis</i>	+	+							
<i>callifolia</i>	+	+							
<i>dura</i>	+	+	+						
<i>henryi</i>	+	+							
<i>longissima</i>	+	+	+						
<i>mucronata</i>	+	+							
<i>novoguineensis</i>	+	+							
<i>platyrynchos</i>	+	+							
<i>revoluta</i>	+	+							
<i>spicata</i>	+	+	+						
<i>validinervis</i>	+	+	+						
<i>Campyloneurum</i>									
<i>angustifolium</i>	+	+	+						
<i>leuconeuron</i>	+	+							
<i>lindigii</i>	+	+							
<i>phyllitides</i>	+	+							
<i>Christiopteris</i>									
<i>sagitta</i>	+								
<i>tricuspidis</i>	+								
<i>varians</i>	+		+						
<i>Colysis</i>									
<i>elliptica</i>		+							
<i>hemionitidea</i>		+							
<i>macrophylla</i>		+							
<i>membranacea</i>		+							

	polo	copolo	anomo	desmo	codesmo	peri	coperi	cyclo	cocyclo
pedunculata	+	+							
poilanei		+							
pothifolia	+	+							
wrightii		+							
Crypsinus	+								
albido-squamatus	+	+	+						
ebenipes	+								
quinquefidum	+	+	+						
rhynchophyllus	+								
stenophyllus	+								
taeniatus	+								
triquetrus	+								
veitchii	+	+	+						
Dendroconche									
annabellae	+	+							
Dendroglossa		+							
minor									
Diblemma		+							
samarensis	+								
Dictymia								++	++
brownii									
mckeel									
Drymoglossum	+	+					+		
pilosoides									
Drymotaenium	+	+		+	+	+			
miyoshianum									
Drynaria	+								
bonii	+	+							
laurentii	+	+	+						
parishii	+		+						
pleuridioides	+	+							
propinqua	+	+							
quercifolia	+	+	+						
rigidula	+								
sparsisora	+	+							
Drynariopsis									
heraclea	+	+	+						

	polo	copolo	anomo	desmo	codesmo	peri	coperi	cyclo	cocyclo
squamulosa	+								
vaccinifolia	+								
Microsorium		+							
hancockii	+	+							
membranaceum	+	+							
musifolium	+	+							
pteropus	+	+							
punctatum	+	+							
sablanianum	+	+							
spectrum	+	+							
tenuilore	+	+							
Neocheropteris									
ensata	+	+							
ensata fo.	+	+							
monstrifera	+	+							
normalis	+	+							
palmatopedata	+	+							
subhastata		+							
Niphidium									
americanum								+	
Oleandropsis									
ferrea	+	+							
Paltonium									
lanceolatum								+	
Paragramma									
balteiformis	+	+							
longifolia	+	+							
Pessopteris									
carinata	+	+							
crassifolia	+	+							
Phlebodium									
aureum	+	+							
decumanum	+	+							
Photinopteris									
speciosa	+	+							
Phymatodes									
commutata	+	+							

[illegible]

	polo	copolo	anomo	desmo	codesmo	peri	coperi	cyclo	cocyclo
Polypodium									
amamianum									
amoenum	+		+						
atkinsonii	+	+							
attenuatum	+	+	+						
australe	+	+	+						
californicum	+								
catharinæ	+								
chnocephorum	+								
crystalloneuron	+	+	+						
falcaria	+	+							
fallax	+	+	+						
fauriei	+	+							
formosana	+	+	+						
fraternum	+	+	+						
fraxinifolium	+	+							
friedrichsthalianum	+	+	+						
gilliesii	+								
lachnopus	+	+							
lepidopteris	+	(+)	+						
loriceum	+	+							
mammeiense	+	(+)							
nipponicum	+								
pellucidum	+	+							
plumula	+	+							
polypodioides	+	+	+						
prairii	+								
pringlei	+	+	(+)						
pyncocarpum	+		+						
scouleri	+	+							
triseriale	+								
virginianum	+	+							
vulgare	+	+							
Pseudodrynaria									
coronans	+	+							
Pycnoloma									
metacoelum	+	+							
murudense	+	(+)							

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ONTOGENY OF DIFFERENT TYPES OF STOMATA

The protoderm cells in a developing leaf are isodiametric, tetrahedral, polygonal, or slightly elongate and uninucleate. These cells can easily be distinguished from the surrounding cells by their smaller size, prominent nucleus, and denser staining cytoplasm. These meristemoids begin to appear long before the main period of meristematic activity in the foliar epidermis is completed. In no species investigated a meristemoid directly functions as the guard cell precursor (guard-cell mother cell). It always cuts off one or two segments before forming two guard cells. All stomata on a leaf do not arise simultaneously. They appear in succession during a considerable period of leaf growth. The sequence of cell divisions in the meristemoids and developments in the neighbouring cells preceding the formation of different types of mature stomata observed in different taxa is noted below.

In *Platycerium ellisii* a considerable number of stomatal meristemoids develop polocytic stomata while a majority of them form copolocytic ones. Those destined to produce polocytic stomata undergo anticlinal division by a curved wall and form two unequal cells (Fig. 2, a and b). The larger daughter cell which is nearer to the proximal end of the leaf, differentiates as a subsidiary cell. The smaller cell has a prominent nucleus and dense staining properties. It soon becomes more or less rounded, and divides by a wall at right angles to the first, forming a pair of guard cells of almost equal size (Fig. 2, c and d).

The guard cells assume a characteristic crescent shape and form the lenticular space between them. Meanwhile the subsidiary cell, which is the sister cell of the guard-cell mother cell, surrounds the proximal pole and the two lateral sides of the guard cells. The cell or cells adjacent to the distal pole of the mature stomata are ordinary epidermal cells derived independently of the stomatal meristemoid (Fig. 2, e). Thus in the polocytic type two cell divisions in the stomatal meristemoid are necessary to produce a mature stoma. The first is arcuate to the distal wall of the

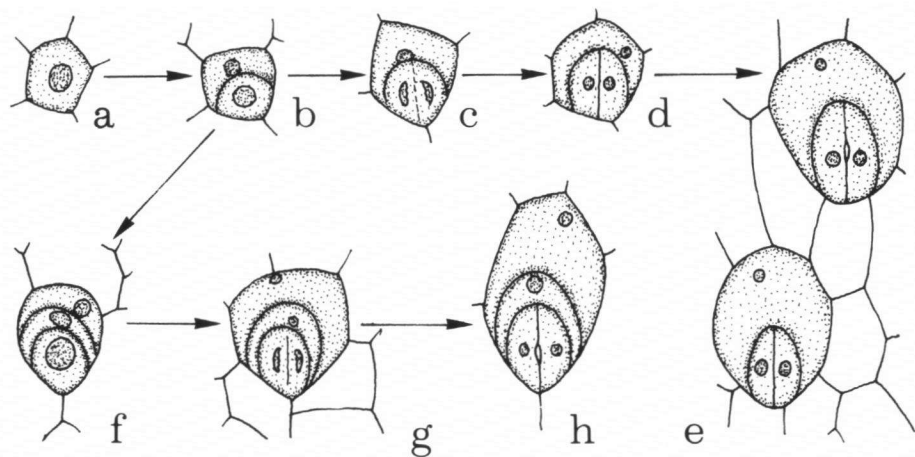


Fig. 2. *Platycerium ellisii*. — Polocytic and copolocytic stomata in stages of development. a, stomatal meristemoid; b, meristemoid after first division; c and d, meristemoids after second division; e, polocytic stomata in early stage of maturation; f, stomatal meristemoid after second division; g, meristemoid after third division; h, copolocytic stoma in early stage of maturation. (All $\times 750$).

stomatal meristemoid and the second is perpendicular to the same wall of the guard-cell mother cell.

The sequence of cell divisions in the stomatal meristemoids forming copolocytic types of stomata is basically similar to that occurring in the meristemoids producing polocytic stomata. The only difference is that in the copolocytic type instead of two divisions in the stomatal meristemoids there are three divisions. As in the polocytic type the meristemoids of the copolocytic stomata first divide into two unequal cells by a curved wall. The smaller daughter cell, instead of functioning directly as the guard-cell mother cell by a wall similar to the first, produces two unequal cells (Fig. 2, f). The first two derivatives of the meristemoids thus produced initiate two subsidiary cells, while the third cell by a wall at right angles to the first and second divisions produce two guard cells (Fig. 2, g and h). As in the polocytic type, the surrounding cells towards the distal region of the guard cells are developed independently of the stomatal meristemoids. In terms of cell alignment this pattern is very similar to the polocytic type.

In *Drynariopsis heraclea* and *Belvisia validinervis* the stomatal meristemoids follow the sequence of cell divisions as are followed by the stomatal meristemoids in *Platycerium ellisii*, and form polo- and copolocytic stomata (Fig. 3, a – e; b, f – h). But in many developing polocytic stomata of these taxa, the subsidiary cell derived from the stomatal meristemoids undergoes one or more anticlinal divisions (Fig. 3, d, i, j; d, i, k). Following such divisions the newly formed cells adjust themselves in such a way that these stomata become anomocytic and it is no more possible to recognise their polocytic nature (Fig. 3, j and l). Interestingly in a few developing copolocytic stomata of these taxa the first subsidiary cell becomes divided by one or more radial anticlinal walls (Fig. 3, g, m – o). Due to new orientation of these cells the stomata no longer retain their copolocytic nature and become polocytic (Fig. 3, o).

In *Platycerium alcinorne* and *P. quadridichotomum* some of the stomatal meristemoids recapitulate all the stages of segmentations followed by a polocytic stoma during its ontogeny, while others follow the stages of cell divisions occurring in a developing copolocytic one (Fig. 4, a – c and e – g). Some of these developing stomata belonging to both the categories soon exhibit further elaborations. A conspicuous lenticular space appears in the inter-cellular material connecting the distal wall of the developing guard cells and surrounding subsidiary cell. Finally the lenticular slit expands bringing about the separation of the wall of the guard cells from that of the subsidiary cell leaving a link at first at two points and later at one point (Fig. 4d and h – i). The adjacent cell or cells situated at the distal end of the desmocytic (with one subsidiary cell at the proximal end; Fig. 4, d) and codesmocytic stomata (with two almost superimposed subsidiary cells at the proximal end; Fig. 4) thus formed, are derived independently from the stomatal meristemoid. The cause of the appearance of the lenticular slit is probably due to the unequal rate of enlargement of the guard cells and the subsidiary cells and their failure in maintaining harmony of mutual readjustments.

The ontogeny of the pericytic type of stomata was studied in *Drymoglossum piloselloides* and *Pyrrosia* sp. (Hennipman 5122). A stomatal meristemoid divides by a curved wall into a large and a small cell (Fig. 4, j). The large cell becomes a subsidiary cell, while the small daughter cell acts as a guard-cell mother cell. The guard-cell mother cell as usual divides by a straight wall almost perpendicular to the wall by which it is separated from the subsidiary cell (Fig. 4, k). The stomatal

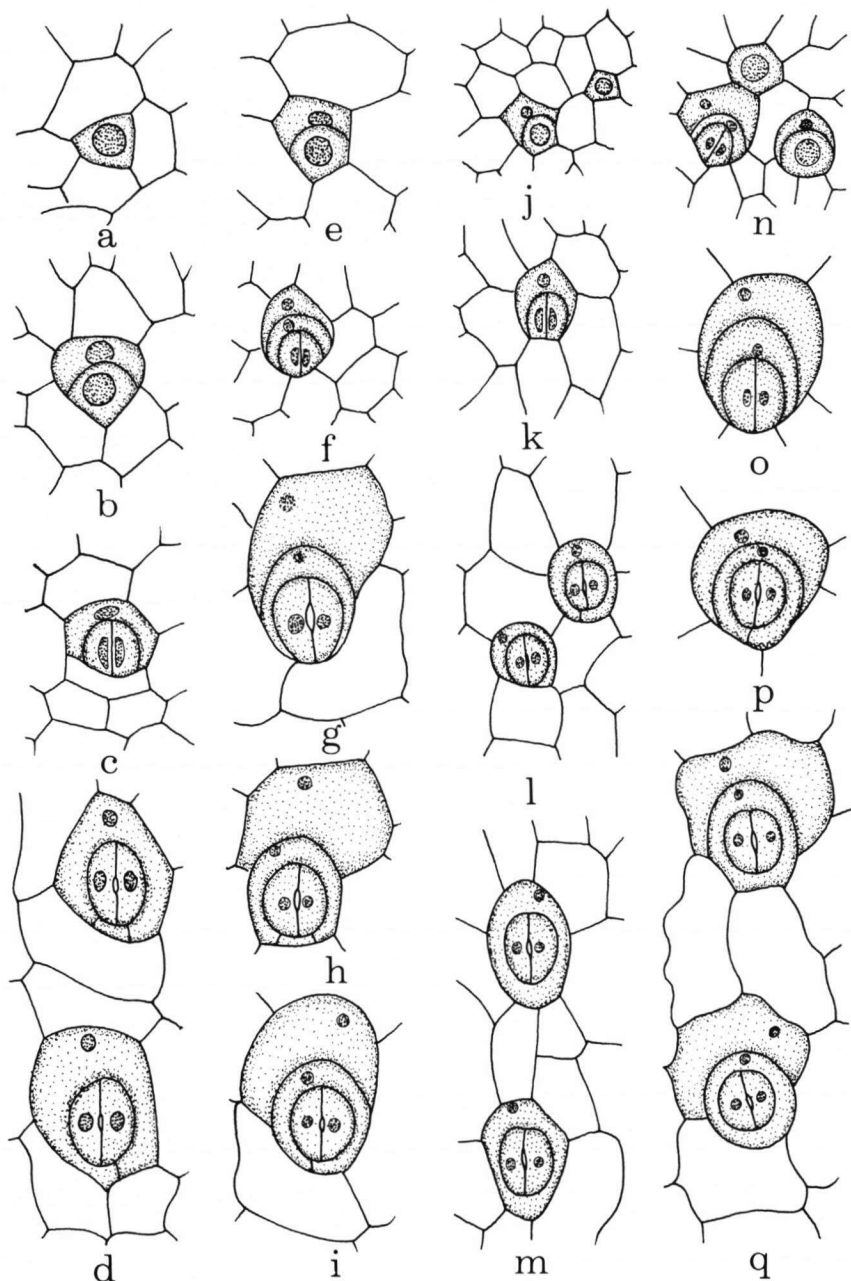


Fig. 4. Pathways of development of desmocytic (a–d), codesmocytic (e–i), pericytic (j–m), and copericytic (n–q) types of stomata. — a–i, *Platycerium alcornae*. — j–m, *Pyrrosia* sp. (Hennipman 5122). — n–q, *Drymoglossum piloselloides*. — (a–c, e, f, j, k, l, n, o, $\times 750$; d, g, h, i, m, p, q, $\times 240$).

meristemoids of these plants upto this stage of development, resemble both in structure and function the stomatal meristemoids of the polocytic stomata. In some of the developing stomata further elaboration is arrested while in others the intercellular substance connecting the walls of guard cells and the subsidiary cell towards the distal end of the leaf swells appreciably and a lenticular space appears within the intercellular material. Then follows the sequence of events that occurs in desmocytic stoma, and the guard cells maintain their contact with the wall of the subsidiary cell just by a short connecting wall (Fig. 4, l). In the final stage of development even this link through a short anticlinal wall is lost in many of them, and the guard cells became completely surrounded by a subsidiary cell (Fig. 4, m).

A few stomatal meristemoids in these taxa (i.e. *Pyrrosia* sp. and *Drymoglossum piloselloides*) instead of developing into pericyclic stomata produce copericyclic ones. These meristemoids divide by a curved anticlinal wall into two unequal cells (Fig. 4, n). The distal cell follows the copolocytic type of development and forms another cell. The smaller of the three cells thus produced behaves as a guard-cell mother cell (Fig. 3, n). The two larger cells, one partly enclosing the other, become subsidiary cells (Fig. 4, o). Following the appearance and increase in size of a lenticular slit in the intercellular material connecting the walls of the guard cells and the inner subsidiary cell, the anticlinal link between them is gradually lost in some of the developing stomata (Fig. 4, o—q). But the two subsidiary cells always maintain their distal periclinal attachment.

The stomatal meristemoids in *Lecanopteris carnosa*, *Lecanopteris sinuosa*, *Dictymia brownii* and *Lemmaphyllum microphyllum* form cyclocytic stomata. During the early stages of development, these meristemoids follow the developmental pathway of polocytic stomata (Fig. 5, a—c). They divide into a smaller daughter cell functioning as guard-cell mother cell and a large cell differentiating into a subsidiary cell. Meanwhile the pair of adjoining epidermal cells flanking the distal end of the stomatal meristemoid undergo longitudinal anticlinal division by straight to curved walls (Fig. 5, d and e). Occasionally these cells become divided by radial walls (Fig. 5, f). These adjoining cells at the distal position together with the subsidiary cell occupying the proximal position form the surrounding cells of the two guard cells. Similar to other surrounding cells, the subsidiary cell itself often undergoes division by a radial wall (Fig. 5, g and h). Sometimes the two neighbouring cells at the distal end of the stomatal meristemoid fail to undergo division preceding, during, or after the initiation of the guard-cell mother cell. But despite their failure to undergo division, they elongate and readjust considerably so as to surround the distal region of the guard cells. The surrounding cells as in all the previous cases are thus of dual origin. The one adjacent to the proximal end is a derivative of the stomatal meristemoid while those at the distal region are of independent origin.

Some of the stomatal meristemoids in *Dictymia brownii*, *Lecanopteris carnosa*, *L. sinuosa* and *Lemmaphyllum microphyllum*, instead of following the polocytic ontogeny, adopt copolocytic development, produce two subsidiary cells, and ultimately form cocyclocytic stomata. The stages of development of a cocyclocytic stoma are shown in Fig. 6, a—f. Occasionally either the inner (Fig. 6, g) or the outer subsidiary cell (Fig. 6) may undergo division by one or more radial periclinal walls increasing the number of cells encircling the guard cells (Fig. 6, g—i, and j—l).

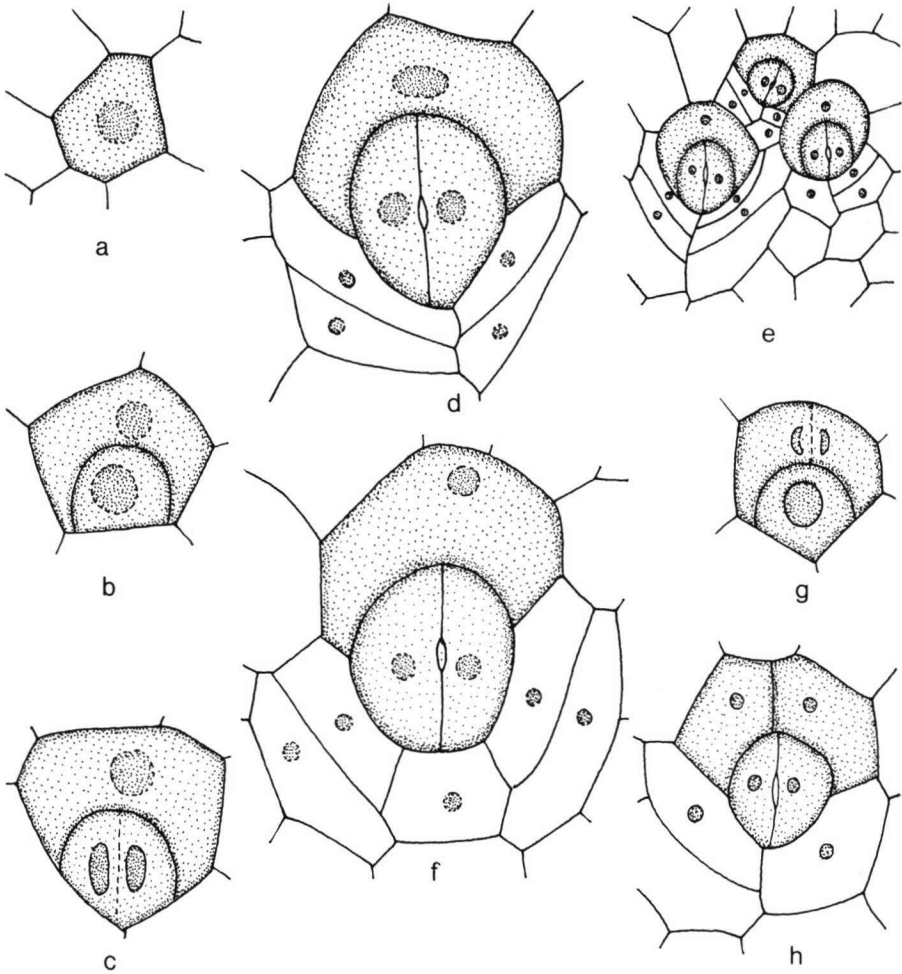
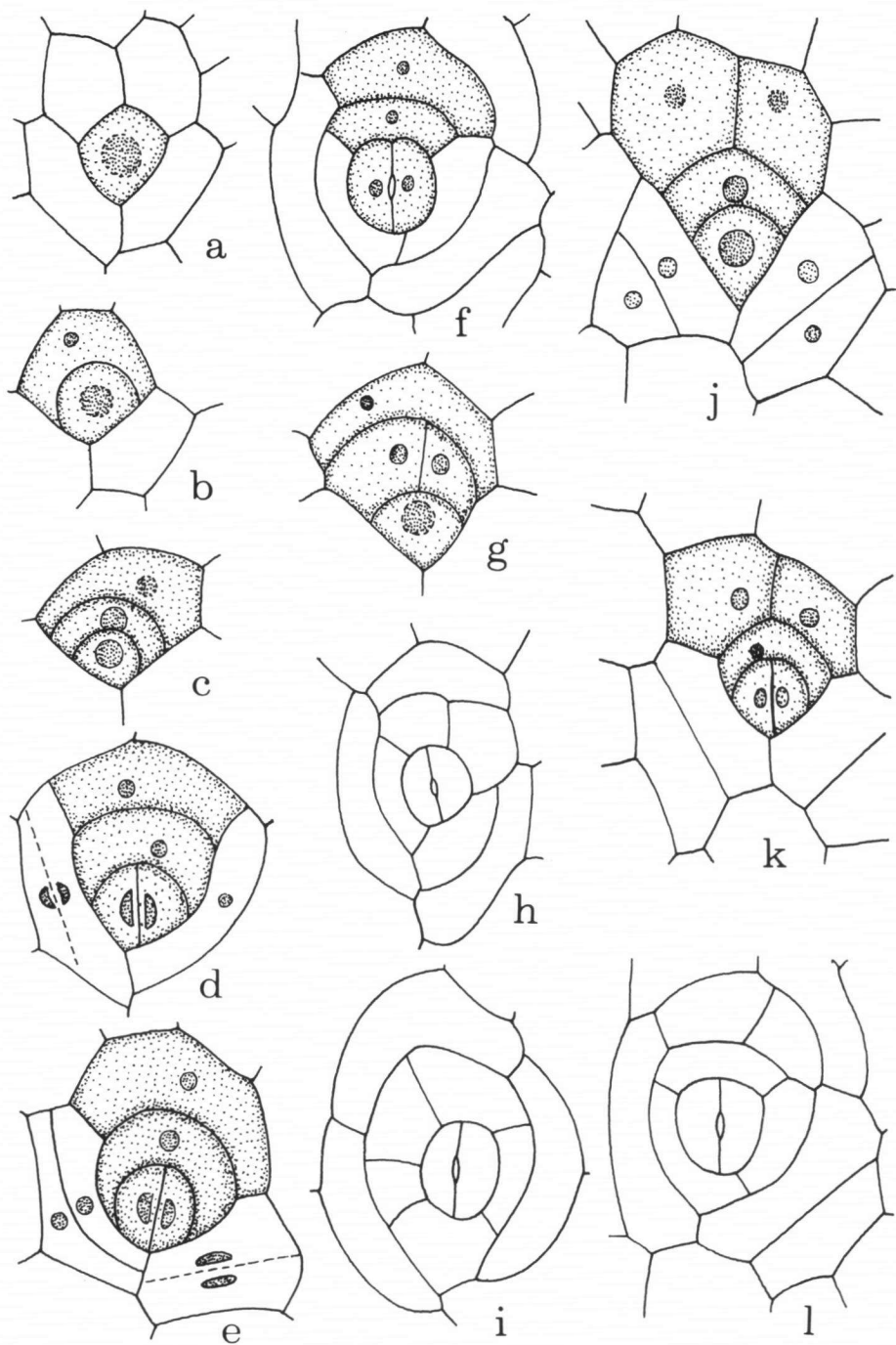


Fig. 5. *Lemnaphyllum microphyllum*. — Cyclocytic stomata in stages of development. a, Stomatal meristemoid; b, meristemoid after first division; c, meristemoid after second division; d–f, guard cells encircled by subsidiary cell at the proximal side and surrounding cells at the distal region; g–h, subsidiary cell with septation. (All $\times 750$).

DISCUSSION AND CONCLUSIONS

Though the adult stomata in the polypodioids exhibit nine sharply defined forms, all of them pass through the polocytic conditions during the course of their development. The polocytic type quite curiously follows an identical pattern of development in three different directions (Fig. 7). In one of these lines of development, leading to the formation of cyclocytic and cocyclocytic stomata, there has been cell division and/or change in orientation in the neighbouring cells



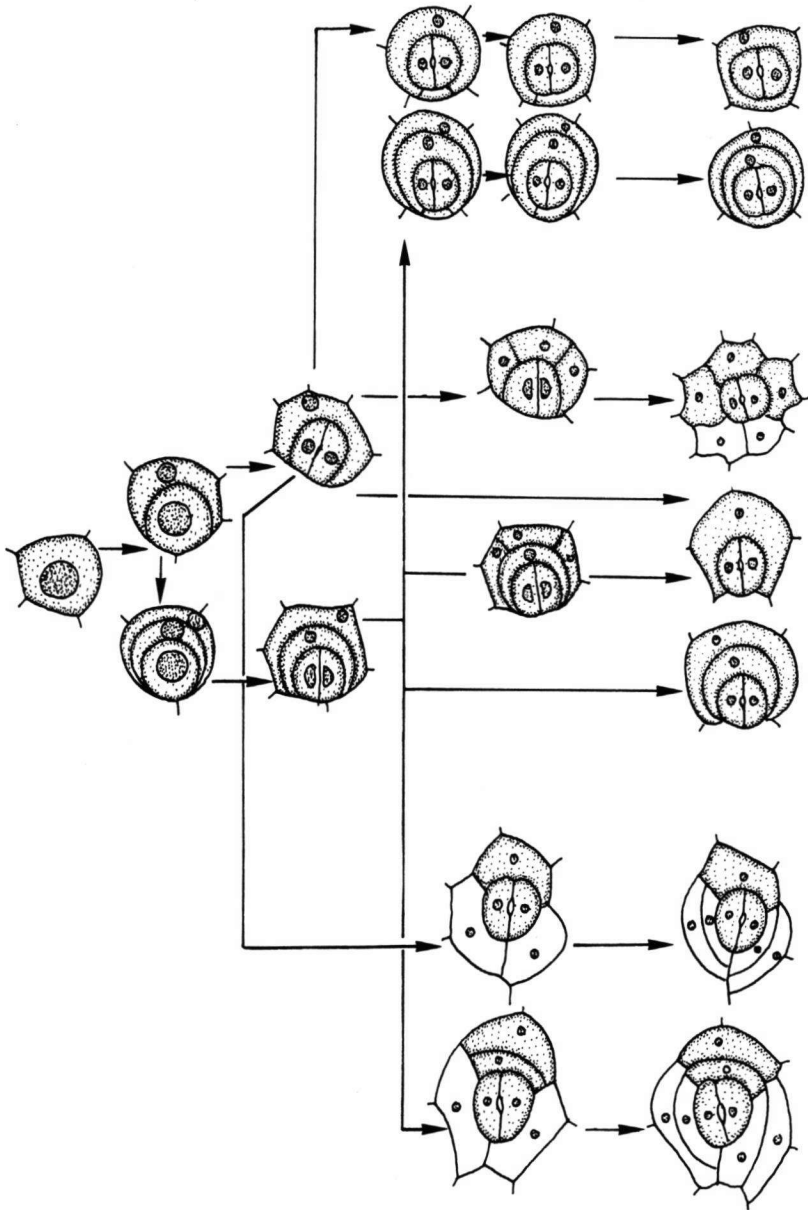


Fig. 7. Different types of polypodioid stomata in stages of development showing ontogenetic interrelationships.

Fig. 6. *Dictymia brownii*.—Cocyclocytic stomata in stages of development. (a – g, j, k, $\times 750$; h, i, l, $\times 240$).

occupying the distal region of the developing stoma. The second line is characterised by the formation of desmo-, codesmocyctic, peri- and copericytic forms. A conspicuous feature of this line is the capacity to breakdown the periclinal wall link between the guard cells and the subsidiary cell. This is probably due to the differential rate of expansion of the guard cells and the associated subsidiary cell or cells at the late stage of their development. Polocytic stomata occurring in mature fronds either arise directly from a juvenile polocytic meristemoid cell which does not further differentiate, or from a 'copolocytic' juvenile cell. The outer subsidiary cell of such a juvenile copolocytic cell undergoes division, and the resulting cells eventually fail to retain their distinctiveness from other epidermal cells. An anomocyctic type of stoma is formed by the division of the subsidiary cell of a developing polocytic stoma. Juvenile copolocytic cells are transformed into polocytic ones as a result of the same phenomenon (i.e. due to the division of the subsidiary cell).

Though the cell surrounding the mature stomata of nine different forms vary considerably, in aspect and or orientation, it is significant that in all these forms they are of dual origin (i.e. mesoperigenous, see Pant, 1965). The surrounding cells or cell adjacent to the proximal region of the stoma are derivatives of the stomatal meristemoid, while those situated at the distal region are derived independently from it. Even in the peri- and copericytic types the stomatal development begins mesoperigenously and appears so until the last anticlinal wall link with the subsidiary cell is lost. It is only after the loss of anticlinal wall contact that the pair of guard cells becomes enclosed by the subsidiary cell derived from the stomatal meristemoid. The mesogenous condition in the adult stage is, therefore, a secondary one. This study thus fails to confirm the view of mesogenous origin of desmocyctic, codesmocyctic, pericytic and copericytic stomata as has been claimed by Fryns-Claessens and Van Cotthem (1973). The observations of Pant (1965) and Mickel and Lersten (1967) that in *Pyrrosia* the guard-cell mother cell is never attached to the surrounding cell could not be confirmed either. Moreover, we found the developmental pathways of the cyclo- and cocyclocytic types of stomata to be very different from the 'cyclomesoperigenous' stomata diagrammed by Fryns-Claessens and Van Cotthem (1973). The cyclo- and cocyclocytic types of stomata in the polypodioids are indeed unique in their mode of development and have never been recorded earlier in any other group of vascular plants.

The results of our studies on stomata are discussed in relation to their possible contribution to establish phylogenetic relationships within the *Polypodiaceae*. As the second author became interested in the cladistic approach to trace phylogenetic relationships already several years ago, due to one of his colleagues in Leiden, Prof. Dr. J. Th. Wiebes, our observations on stomata will be analysed according to the idea set forth by Hennig (1966). In a forthcoming monograph of the fern genus *Platyserium* (Hennipman and Roos, in preparation) Hennig's ideas are successfully applied to establish phylogenetic relationships within the genus, using a large number of characters.

According to the cladists, monophyletic groups can be based on shared apomorphic (derived) character states only. Groups based on shared plesiomorphic (primitive) character states are in principle heterogeneous. Hennig's ideas have been mainly applied to zoological groups. Only recently botanists have become interested in his theory (e.g. Bremer and Wanntorp, 1978).

The establishment of the most likely apomorphic character state of stomatal

types is a prerequisite for the application of the cladistic methodology. When looking at the chart depicting the ontogenetic relations between these types of stomata, it can be supposed that cyclo- and cocyclocytic stomata, as well as the peric- and copercicytic and the allied desmo- and codesmocytic types, represent two different apomorphic states easily differentiated from the polo- and copolocytic conditions. Cyclo- and pericytic stomata never occur together which in itself indicates their different evolution.

The plurality of the polypodiaceous ferns shows the combined appearance of polo- and copolocytic stomata as could be expected from a plesiomorphic condition. Polocytic stomata occur very commonly not only in the *Polypodiaceae* but also in *Grammitidaceae*, a family we regard the most likely sistergroup.

The second possibility of plesiomorphic condition refers to either the pericytic or the cyclocytic stomata, from which the polo- and copolocytic stoma arose through retention. This seems however unlikely since such a transformation series would have involved retention combined with subsequent radiation.

It should be remarked that the interpretation of the polocytic stoma is twofold. The fact that an originally copolocytic stoma may become polocytic again through cell division and orientation makes it difficult to ascertain whether the polocytic state as found in the adult stage is 'real' polocytic or 'pseudo' polocytic.

The following groups of genera share one of the apomorphic stomatal types recognised, or are primarily classified because of the occurrence of copolocytic stomata only. These groups can be regarded as monophyletic groups unless parallelism has taken place.

1. The genera *Drymoglossum*, *Platycerium*, *Pyrrosia*, and *Saxiglossum*

Recent research by Price (1974) and Hennipman and Ravensberg (in preparation) has shown that the genus *Drymoglossum* (syn.: *Pteropsis*) is synonymous with *Pyrrosia*. The same is true for *Saxiglossum*. The stomatal types confirm this. The stomatal types as well as other features (e.g. stellate hairs) point to a relationship between *Pyrrosia* and *Platycerium*. Such a relationship has been questioned by several authors. Ching (1940) accommodated *Platycerium* in a separate family *Platyceriaceae*, while Pichi Sermolli (1977) placed these two genera in different groups of *Polypodiaceae*. On the other hand, the spores of *Pyrrosia* and *Platycerium* have in part a strikingly different perispore (Hennipman and Sen, in preparation).

2. The genera *Dictymia*, *Dicranoglossum* (syn.: *Eschatogramma*), *Lecanopteris*, *Lemmaphyllum*, *Niphidium*, and *Paltonium* (syn.: *Neurodium*)

According to slight differences in stomatal types this group can be subdivided into three different subgroups which are mutually not closely related as far as present knowledge is concerned, obviously representing three different parallel developments.

2a. *Dicranoglossum*

The stomata as found in *Dicranoglossum* (syn.: *Eschatogramma*) are different from those found in the other groups showing an incomplete orientation of surrounding cells towards the distal region. The occurrence of this condition suggests that cyclo- and cocyclocytic stomata are liable to parallel evolution.

2b. The genera *Dictymia*, *Lecanopteris* and *Lemmaphyllum*

It is striking that the stomatal types of *Lemmaphyllum* and those of *Pleopeltis* species with polypodioid sori as listed by Copeland (1947), have a derived type of

stoma. In *Weatherbya*, Van Cotthem (1970a) found that some of the polocytic stomata have a cyclocytic appearance because of an additional periclinal division of the cells. *Lemmaphyllum* s.l. is presently under study in our group by Mr. J. van Scheepen.

The data further support the idea to recognize a large genus *Lecanopteris*, thus including *Myrmecopteris* (Jermy and Walker, 1975). Other authors keep these genera separate because of salient differences in rhizome indument (e.g. Pichi Sermolli, 1977). Holtum (1954) accommodated the species of *Myrmecopteris* in *Phymatodes*. Pichi Sermolli relates *Solanopteris* to *Lecanopteris*, which is not confirmed. Further research on other features may show whether the stomatal similarity in *Dictymia*, *Lecanopteris* s.l., and *Lemmaphyllum* is due to monophyly or parallelly.

2c. *Niphidium* and *Paltonium*

In spite of the occurrence of exclusively cyclocytic stomata in *Niphidium* and *Paltonium*, the relationship between these genera is not obvious, due to some other structural differences. Future research is necessary to ascertain whether this similarity in stomatal feature is homoplastic or otherwise.

3. The microsorioid ferns

When checking the stomatal types in the remaining genera we see that the combination of polo- and copolycytic stomata is the rule in most of the taxa studied. In case this is the plesiomorphic condition, polypodioid ferns having but one type of stoma are necessarily derived. The polocytic as well as the copolocytic type of stomata both can occur singly. The anomocytic stoma always occurs in association with the polocytic stoma and sometimes also with the copolocytic one.

A. Exclusively polocytic stomata are found in two species of *Christiopteris*, three species of *Crypsinus*, *Holcosorus bisulcatus*, *Holostachyum buchananii*, two species of *Microgramma*, *Paragramma balteiformis*, *Pleopeltis scolopendria*, two species of *Pycnoloma*, and *Synammia feuilli*. Polocytic stomata in association with copolo- and anomocytic stomata occur in five species of *Belvisia*, *Campyloneuron leuconeuron*, *Christiopteris tricuspsis*, two species of *Crypsinus*, three species of *Drynaria*, *Drynariopsis heraclea*, *Goniophlebium demersum*, two species of *Microgramma*, *Pleopeltis excavata*, fourteen species of *Polypodium*, *Selliguea feei*, and the *Solanopteris* species investigated.

In the genera *Christiopteris* and *Solanopteris* copolocytic stomata were found to be absent.

B. Species with copolocytic stomata only are found in *Colysis* (six out of eight species investigated), *Dendroglossa minor* (syn.: *Leptochilus minus*; *Colysis minor*), *Neochiropteris subhastata*, and *Podosorus angustatus* (syn.: *Polypodium prainii*). Other species of these genera have the combination of polo- and copolocytic stomata. Thus, the genera share the condition that with increased specialisation of the stomata forming processes, the formation of polocytic stomata is suppressed. These genera, together with the genera closely related to them for other reasons, having species with both polo- and copolocytic stomata and never having anomocytic stomata, e.g. *Leptochilus*, *Paraleptochilus*, *Diblemma*, and *Microsorium*, should be treated together.

It is tempting to discuss these two different types of stomata in relation to primitive and derived states. The taxa with polocytic stomata only or with polocytic stomata associated with copolo- and anomocytic stomata include the drynarioid ferns, the genera related to *Crypsinus*, and a number of genera whose relationship is

otherwise still obscure; the genera assembled in group A obviously do not constitute a natural group. This is in sharp contrast with the genera of group B, which are unmistakably microsorioid. This being true, the stomata forming process that occurs in the genera of group A should represent the original condition in the family. This hypothesis is strongly supported by the fact that in the *Grammitidiaceae*, the possible sister group of the *Polypodiaceae*, polo- and anomocytic stomata are the rule (Van Cotthem, 1970a). The fact that the more specialised stomatal types as listed in group 1 and group 2 sometimes occur in association with polocytic stomata, or with polo- and copolocytic stomata, but never with copolocytic stomata alone may represent a second argument. It is further noteworthy that the specialised types of stomata never occur in association with anomocytic stomata.

In this connection we should like to mention that the observation of Van Cotthem (1970a) that the combination of polocytic and anomocytic stomata does not occur in the *Polypodiaceae* could not be confirmed. Van Cotthem (1970a) followed by Pichi Sermolli (1977), used the stomatal features in distinguishing *Grammitidaceae* and *Loxogrammaceae* from the *Polypodiaceae*, which could not be confirmed either.

In conclusion, the analysis of the stomata types in a large number of taxa of *Polypodiaceae*, together with a study of the ontogeny of a selection of polypodioid species, gives strong evidence for the recognition of a number of possible natural groups. The groups suggested are only in part congruent with the groups recognized within the *Polypodiaceae* recently by authors including Crabbe et al. (1975) and Pichi Sermolli (1977).

If compared with the subfamilies listed by Crabbe et al. (1975), our data suggest that apart from the subfamilies *Drynarioideae* and *Platyserioideae*, the remaining three subfamilies are markedly heterogeneous.

In the publication of Pichi Sermolli (1977) the *Polypodiaceae* are subdivided into 14 groups, five of which consisting of one genus only. Amongst these is the genus *Christiopteris* which, because of an erroneous observation by Van Cotthem (Van Cotthem, 1970a) is ranked by Pichi Sermolli (1977) as a genus of doubtful reliance. Of the remaining 9 groups, the groups represented by *Pyrrosia*, *Drymoglossum*, and *Saxiglossum* (which are congeneric in our opinion) and the drynarioid ferns, are unambiguously monophyletic groups. If we compare the remaining seven groups which contain 46 out of 63 genera recognized by Pichi Sermolli, with the groups as suggested here, four groups recognized by Pichi Sermolli are likely to be heterogeneous.

It is indeed gratifying to be able to point to the undoubted usefulness of the stomatal features in determining some phylogenetic affinities in these plants, and the perspective of the methodology applied. Of course, this study is only a first step towards solving many a phylogenetic problem in the family.

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LIST OF SPECIES STUDIED

- Aglaomorpha meyeniana* Schott (*Ramos* BS 13649, L)
- A. splendens* (J. Sm.) Copel. (*Hoogland* 6257, L)
- Anapausia decurrens* (Bl.) Presl (*Hennipman* 3836a, L; *Phengkhlai* 37, L, *T. Shimizu et al.* T 11386, L)
- Artromeris himalayense* (Hook.) Ching (*Gammie* 700, L)
- A. lehmanni* (Mett.) Ching (*Dickason* 8104, L)
- A. wallichiana* (Spring) Ching (*Mann s.n.*, L)
- Belvisia callifolia* (Christ) Copel. (*Poilane* 12210, L; *Kostermans s.n.*, 12.1.1969, L)
- B. dura* (Copel.) Copel. (*St. John & Maireau* 15621, UC)
- B. henryi* (Hieron. ex C. Chr.) Raymond (*Hennipman* 3376, L)
- B. longissima* Holtum (*Brass* 30362, L)
- B. mucronata* (Fée) Copel. (*Kjellberg* 1422, L)
- B. novoguineensis* (Ros.) Copel. (*Brass* 30462, L)
- B. platyrhynchos* (Kunze) Copel. (*McClure* BS 16058, C)
- B. revoluta* (Bl.) Copel. (*Holstvoogd* 226, L)
- B. spicata* (L.f.) Mirbel ex Copel. (*Wild* 6571, M)
- B. validinervis* (Kunze) Copel. (*Hennipman* 5541, cult. Leiden Bot. Garden; *Edaño* PNH 860, L)
- Campyloneurum angustifolium* (Sw.) Fée (*Pringle* 8979, L; *Hatschbach* 10257, L)
- C. leuconeuron* Fée (*Buchtien s.n.*, L 9137331)
- C. lindigii* (Mett.) Ching (*Schlim* 440, L)
- C. phyllitides* (L.) Presl (*Van Lansbergen* 65, L)
- Christiopteris sagitta* (Christ) Copel. (*Copeland s.n.*, P)
- C. tricuspis* (Hook.) Christ (*Hennipman* 3678, L)
- C. varians* (Mett.) Copel. (*Franc* 686, L)
- Colysis elliptica* (Thunb.) Ching (*Hennipman* 3391, L)
- C. hemionitidea* (Wall. ex Mett.) Presl (*Tagawa* 1938, L)
- C. macrophylla* (Bl.) Presl (*Lörzing* 12370, L)
- C. membranacea* (Bl.) Presl (*Merrill* 10493, L)
- C. pedunculata* (Hook. et Grev.) Ching (*Hennipman* 3881, L)

- C. poilanei* C. Chr. & Tard. (*Poilane* 32103, P)
C. pothifolia (Don) Presl (*Tagawa* 7871, L)
C. wrightii (Hook.) Ching (*Fosberg* 37472, L)
Crypsinus albido-squamatus (Bl.) Copel. (*Elmer* 22107, L)
C. ehenipes (Hook.) Copel. (*Polunin et al.* 5451, L)
C. quinquefidum (Bak.) ined. (*Meijer* 612, L)
C. rhynchophyllus (Hook.) Copel. (*Brass* 31635, L)
C. stenophyllus (Bl.) Holttum (*Meijer* 2471, L)
C. taeniatus (Sw.) Copel. var. *palmatus* (Bl.) C. Chr. (*Forster* 203, L)
C. triquetrus (Bl.) Copel. (*de Wilde & de Wilde-Duyffes* 15281, L)
C. veitchii (Bak.) Copel. (*Maire s.n.*, L 91842127)
Dendroconche annabellae (Forbes) Copel. (*King* 206, BO)
Dendroglossa minor (Fée) Copel. (*Brass* 25074, L; *M. Ramos* BS 20400, L)
Diblemma samarensis J. Sm. (*Edaño* BS 15133, BO)
Dictymia brownii (Wikstr.) Copel. (cult. Leiden Bot. Garden; *Constable* NSW 8009, L)
D. mckeei Tindale (*Lam* 7219, L)
Drymoglossum piloselloides Presl (cult. Leiden Bot. Garden)
Drymotaenium miyoshianum (Mak.) Makino (*Umemura s.n.*, L 961244621)
Drynaria bonii Christ (*Larsen* 10634, L)
D. laurentii (Christ) Hieron. (*Leeuwenberg* 3088, L)
D. parishii (Bedd.) Bedd. (*Larsen et al.* 3025, L)
D. pleuridioides Presl (*Lörzing* 15268, L)
D. propinqua (Wall.) ex Mett. J. Smith (*Henry* 13092, L)
D. quercifolia (L.) Sm. (*Lam* 3386, L)
D. rigidula (Sw.) Bedd. (*Franc* 33, L)
D. sparsisora (Desv.) Moore (*Hennipman* 3949, L)
Drynariopsis heraclea (Kunze) Ching (*Rutten* 1963, L; cult. Leiden Bot. Garden)
Eschatogramma desvauxii (Kl.) C. Chr. (*Terpstra* 35, L)
E. furcata (L.) C. Chr. (*Witte s.n.*, L 936224372)
Goniophlebium demersum (Brause) Copel. (*Croft et al.* LAE 60621, L; *Schodde* 1438, L)
G. korthalsii (Mett.) Bedd. (*Korthals s.n.*, L 908294531; *Rosenstock* 14722, L)
G. persicifolium (Desv.) Bedd. (*Elmer* 11631, L; *Sürbeck* 720, L)
G. subauriculatum (Bl.) Presl (*Hennipman* 3363, L; 3449, L)
G. truncato-sagittatum (Brause) ined. (*Pulle* 1126, L)
G. verrucosum (Hook.) J. Sm. (*Brass* 7672, L; *Croft & Lelean* LAE 65608, L; *Lam* 708, L)
Grammatopteridium costulatum (Ces.) C. Chr. var. *costulatum* (*Lam* 826, L)
G. costulatum (Cesati) C. Chr. var. *beguinii* (v.A.v.R.) C. Chr. (*Brass* 11699, L)
G. costulatum (Ces.) C. Chr. var. *brooksii* (v.A.v.R.) C. Chr. (*Brooks* 361, S., BO)
Holcosorus bisulcatus (Hook.) Copel. (*Brass* 12791, L)
Holostachyum buchananii (Copel.) Ching (*Floyd* 5241, L)
Lecanopteris carnosa (Reinw.) Bl. (cult. Leiden Bot. Garden)
L. lomarioides (Brause) Baker (*Meijer* 2511, L)
Lemmaphyllum carnosum (Wall.) Presl (*Forrest* 18924, W; *Mann s.n.*, L 908338568)
L. drymoglossoides (Bak.) Ching (*Cavalerie* 627, L; *Maire* 17428, W)
L. microphyllum (cult. Leiden Bot. Garden; *Gaudichaud* 33, G; *Tagawa* 8612, UC)
L. microphyllum Presl var. *obovatum* (Harr.) Presl (*Warburg* 10937, B)
L. rostratum (Bedd.) Tagawa (*Rosenstock* Fil. formos. exsicc. 172, MICH; *Mann s.n.*, L 90828829; *de Wilde & de Wilde-Duyffes* 13702, L)
Microgramma ciliata (Willd.) Copel. (*Burchell* 9779, L)
M. heterophylla (L.) Wherry (*Smith et al.* 3256, L)
M. lycopodioides (L.) Copel. (*Columb* 152, L)
M. persicariifolia (Schrader) Presl (*Broadway* 2402, L)
M. piloselloides (L.) Copel. (*Hatschbach* 17178, L; *Herzog* 2153, L; *Ule* 6517, L)
M. squamulosa (Kaulf.) ined. (*Petersen & Hjerting* 659, L)
M. vacciniifolia (Langsd. & Fisch.) Copel. (*Anonymus*, L 908289452, L)
Microsorium hancockii (Baker) Ching (*Hansen & Smitinand* 12806, L)
M. membranaceum (Don) Ching (*Tagawa* 3721, L)
M. musifolium (Bl.) Copel. (*Jacobs* 5070, L)
M. pteropus (Bl.) Copel. (*Hennipman* 3955, L)
M. punctatum (L.) Copel. (*Hennipman* 3065, L)
M. sablanianum (Christ) Copel. (*Brooke* BAU 9869, L)
M. spectrum (Kaulf.) Copel. (*H. L. & M. F. Lyon* 1169, L)
M. tenuilore (J. Sm.) Copel. (*Iwatsuki et al.* 1200, L; *Hennipman* 5618 (fixed material, L); 5619 (fixed material, L))
Neocheiropteris ensata (Thunb.) Ching (*Oldham, s.n.*, L 908300530)
N. ensata (Thunb.) Ching fo. *monstrifera* (Tagawa) Tagawa (*Tagawa & Iwatsuki* 3635, L)
N. normalis Don Tagawa (*Hennipman* 3393, L)
N. palmatopedata (Bak.) Christ (*Kouy-tch* 4162, L)
N. subhastata (Baker) Tagawa (*Rosenstock, Filices chinenses* exsicc. 113, L)

- Niphidium americanum* (Hook.) J. Sm. (*Rose* 22816, US)
Oleandropsis ferrea (Brause) Copel. (*Brass* 12795, L)
Paltonium lanceolatum (L.) Presl (*Eggers* 259, L)
Paragramma balteiformis (Brause) Copel. (*Brass* 12075, UC)
P. longifolia (Bl.) Moore (*Meijer* 1110, L)
Pessopteris carinata (Lellinger) ined. (*Buchtien* s.n., L)
P. crassifolia (L.) Underw. & Maxon (*Wright* 1022, L)
Phlebodium aureum (L.) Sm. (*Boom* 21075, L)
P. decumanum J. Sm. (*Schlim* 153, L)
Photinopteris speciosa Bl. (*Lam* 6672, L)
Phymatodes commutata (Bl.) Ching (*Croft LAE* 60581, L)
P. diversifolium (Willd.) Pic. Serm. (*Varekamp* 6, L)
P. nigrescens J. Sm. (*Brass* 23887, L)
P. scolopendria (Burm.) Ching (*Nedi & Idjan* 164, L; *Schmutz F-9*, L)
Platyserium alaicorne Desv. (cult. Leiden Bot. Garden)
P. andinum Baker (cult. Leiden Bot. Garden)
P. bifurcatum (Cav.) C. Chr. ssp. *bifurcatum* var. *bifurcatum* (cult. Leiden Bot. Garden)
P. coronarium (König ex Muller) Desv. (cult. Leiden Bot. Garden)
P. elephantotis Schweinf. (cult. Leiden Bot. Garden)
P. ellisii Bak. (cult. Leiden Bot. Garden)
P. grande (Fée) Kunze (cult. Leiden Bot. Garden)
P. bifurcatum ssp. *bifurcatum* (Cav.) C. Chr. var. *hillii* (Moore) ined. (cult. Leiden Bot. Garden)
P. holttumii De Jonch. & Hennipm. (cult. Leiden Bot. Garden)
P. madagascariense Baker (cult. Leiden Bot. Garden)
P. quadridichotomum (Bonap.) Tardieu (cult. Leiden Bot. Garden)
P. ridleyi Christ (*Henderson* 22617, C)
P. stemaria (Beauv.) Desv. 'var. *delaurentii* De Wild.' (cult. Leiden Bot. Garden)
P. stemaria (Beauv.) Desv. (cult. Leiden Bot. Garden)
P. superbum De Jonch. & Hennipm. (cult. Leiden Bot. Garden)
P. bifurcatum (Cav.) C. Chr. ssp. *veitchii* (Und.) ined. (cult. Leiden Bot. Garden)
P. wallichii Hooker (cult. Leiden Bot. Garden)
P. wandae Racib. (cult. Leiden Bot. Garden)
P. bifurcatum (Cav.) C. Chr. ssp. *willinckii* (Hooker) ined. (*Van Steenis* 1822, L)
Pleopeltis abbreviata (Fée) (*Poillane* 7939, P)
P. astrolepis Liebm. (*Heller* 6300, L)
P. bicolor (Takeda) Sledge (*Polunin et al.* 4894, L)
P. elongata Kaulf. (*Degener & Parks, s.n.*, 23.6.1933, L)
P. excavata (Bory) Moore (*Lam & Meeuse* 5334, L; *Maas Geesteranus* 4916, L; 5781, L)
P. loriforme (Wall. ex Mett.) Alston & Bonner (*Ludlow et al.* 16058, L)
P. macrocarpa (Bory ex Willd.) Klif. (*Maas Geesteranus* 6311, L)
P. schraderi (Mett.) Tardieu (*Jacobs* 8535, L)
P. scolopendria (Don) Alston et Bonner (*Hennipman* 3151a, L)
P. sinensis (Christ) Copel. (*Iwatsuki et al.* T 9586, L)
P. thunbergiana Kaulf. (*Dorsett & Morse* 674, L; *Fosberg* 37302, L; *Moran* 42600, L)
Podosorus angustatus Holttum (*Gutierrez PNH* 78332, L)
Polypodiopsis brachypoda (Copel.) Copel. (*J. & M. S. Clemens* 32467, L)
P. colorata Copel. (*Bell* 2019, L)
Polypodium amamianum Tagawa (*Koidzumi s.n.*, 5.5.1923, L)
P. amoenum Wall. ex Mett. (*Iwatsuki et al.* T 9581, L; *Shimizu et al.* 11465, L)
P. atkinsonii C. Chr. (*Ludlow et al.* 19615, L)
P. attenuatum H. B. Willd. (*Splitgerber* 374, L)
P. attenuatum H. B. Willd. var. *gladitum* (*Buchtien s.n.*, L 910211377)
P. australe Fée (*De Joncheere MAD* 134, L; *Nijhoff & Sinnema* 20, L; *Sandwith* 2016, L)
P. californicum Kaulf. (*Heller* 5011, L)
P. catharinae Langsd. et Fisch. (*E. O. Müller s.n.*, L 90912309)
P. chnoophorum Kze (*Balansa* 2878, L)
P. crystalloneuron Ros. (*Buchtien s.n.*, L 9137207)
P. falcaria Kze. (*Bourgeau* 3187, L)
P. fallax Schlecht. & Cham. (*Bourgeau* 1831, L)
P. fauriei Christ (*Tagawa* 8500, L)
P. formosana (Bak.) Nakai (*Tagawa* 7940, L)
P. fraternum Schlecht. et Cham. (*Pringle s.n.*, L 90910270)
P. fraxinifolium Jacq. (*Hatschbach* 17495, L)
P. friedrichsthalianum Kunze (*Stork* 4794, L)
P. gilliesii C. Chr. (*Gerth* 16, L)
P. lachnopus Wall. ex Hook. (*Bor* 16265, L)
P. lepidopteris (Langsd. et Fisch.) Kze. (*Boom* 27412, L; *Hennipman* 4146, L; *Witte s.n.*, L 936224342)
P. loriceum L. (*Kitts s.n.*, L)
P. mammeiense Christ (*Tagawa et al.* T 1507, L)
P. nipponicum Mett. (*Tagawa* 7538, L)
P. pellucidum Kaulf. (*Degener & Degener* 30703, L; *Heller* 2075, L)
P. plumula H. B. Willd. (*Arsène s.n.*, L 913153591)
P. polypodioides (L.) Hitchcock (*Rosenstock det. no.* 16336, L)
P. prainii (Bedd.) C. Chr. (*Schimizu et al.* 13254, L)

- P. pringlei* (Maxon) C. Chr. (*Pringle* 11855, L)
P. pycnocarpum C. Chr. (*Herzog* 2332, L)
P. scouleri Hook. & Grev. (*Rose* 66081, L)
P. triseriale Sw. (*Smith* 2564, L)
P. virginianum L. (*Rolland* — *Germain* 6013, L)
P. vulgare L. (*Pauca* 1637a, L)
Pseudodrynaria coronans (Wall. ex Mett.) Ching (*Hennipman* 3995, L)
Pycnoloma metacoelum (v.A.v.R.) C. Chr. (*Hallier* 2942, L)
P. murudense C. Chr. (*J. & M. S. Clemens* 33980, L)
P. rigidum (Hook.) C. Chr. (*Hirano & Hotta* 163, L)
Pyrrosia species (*Hennipman* 5122, cult. Leiden Bot. Garden)
P. abbreviata (Zoll.) Ching (*Kostermans* 22122, L)
P. longifolia (Burman) Morton (*Van Royen* 4549, L)
P. lanceolata (L.) Farwell (*Tagawa* 2904, L)
P. angustata (Sw.) Ching (*Bunnemeijer* 6802, P; *De Wilde & De Wilde-Duyffes* 19544, L)
P. confluens (R. Br.) Ching (*Lam* 7660, L)
P. dimorpha (Copel.) Parris (*Hoogland* 4173, L)
P. floccigera (Bl.) Ching (*Hennipman* 3814, L)
P. flocculosa (Don) Ching (*Hennipman* 3352, L)
P. foveolata (Alston) Morton (*Van Royen* 4315, L)
P. gralla (Gies.) Ching (*Tagawa* 3023, L)
P. heteractis (Mett. ex Kuhn) Ching (*Hennipman* 3831, L)
P. lingua (Thunb.) Farw. (*Togashi* 447, L)
P. stictica (*Hennipman* 3350, L)
P. mollis (Kunze) Ching (*Surbeck* 1012, L)
P. nummularifolia (Sw.) Ching (*Jacobs* 8407, L)
P. princeps (Mett.) Morton (*Brass* 23703, L; *Van Royen* 5189, L)
P. rupestris (R. Br.) Ching (*Evans* 2478, L)
P. serpens (Forst. f.) Ching (*Bernardi*, L)
P. shearer (Bak.) Ching (*Tagawa* 109, L)
P. sphaerosticha (Mett.) Ching (*Van Borssum Waalkes* 1668, L)
P. stigmata (Sw.) Ching (*Van Borssum Waalkes* 293, L; *Hennipman* 3015, L)
P. species (*Hennipman* 5122, L)
Saxiglossum taenioides (C. Chr.) Ching (*Fan & Li* 702, L)
Selliguea feei Bory (*Kostermans* 293, L)
S. lima (v.A.v.R.) Holtt. (*Iwatsuki et al.* S 1068, L)
Solanopteris brunei (Wercklé ex Christ) Wagner (*Liesner* 662, L)
S. bifrons (Hooker) Copel. (*Cuatrecasas* 11209, US)
Synammia feuillii (Bert.) Copel. (*Lam* 7885, L)
Thayeria cornucopia Copel. (*Copeland s.n.*, UC 769060)
Thylacopteris diaphana (Brause) Copel. (*Brass* 12838, L; *Schlechter* 18220, L)
T. papillosa (Bl.) Kze. (*Anderson S.* 29900, L)
Weatherbya accedens (Bl.) Copel. (*Elmer* 9721, L)
W. damunensis (Ros.) Copel. (*Schlechter* 14399, G)